Fig. 1.

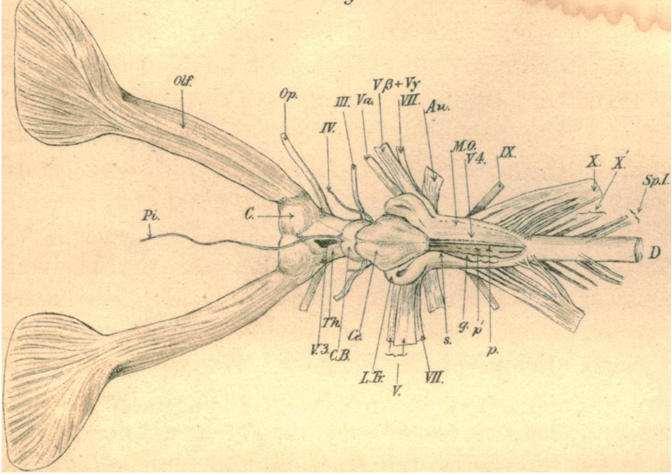


Fig. 3.

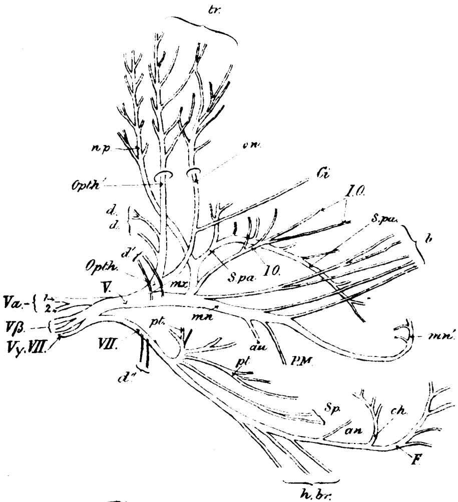
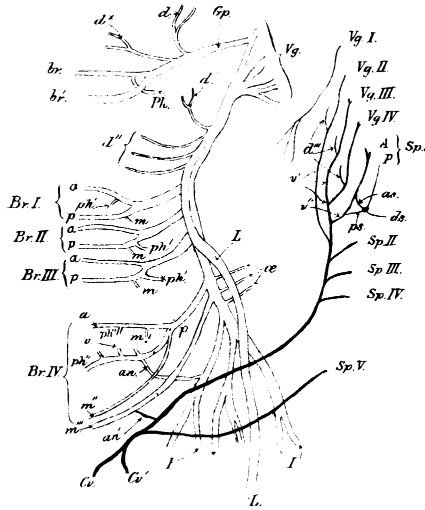


Fig. 2.



NERVES OF ECHINORHINUS. P. 107.

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THE BRAIN AND CRANIAL NERVES OF ECHINORHINUS SPINOSUS, WITH NOTES ON THE OTHER VISCERA. By WM. HATCHETT JACKSON, B.A., F.L.S., *New College*, and WM. BRUCE CLARKE, B.A., *Burdett-Coutts Scholar, Pembroke College, Demonstrators of Anatomy, University Museum, Oxford*[1] [Pl. VII.].

SINCE the commencement of the present year, the Anatomical Department of the University Museum, Oxford, has received two specimens, both in a very good state of preservation, of the rare shark, Echinorhinus Spinosus. One specimen, a fine female, was captured on Feb. 15th, 1875, in Mount's Bay, Penzance, by a fisherman without any aid, a rather remarkable feat. It was received at the Museum, Feb. 20th, and dissected the same day, having kept exceedingly well; a circumstance probably due in part to the great cold then prevailing, in part, perhaps, to the deep-sea habitat of the fish. The other specimen, a male, was also caught at Penzance on Tuesday night, May 4th, and was dissected the following Saturday. The respective dimensions of the two sharks were as follows:—

	Male		Female.	
Tip of snout to end of tail	5 ft.	1 in.	7 ft.	8 in.
Snout to nostril			0	6
„ eye	0	5⅛	0	7
„ spiracle	0	9	1	0½
„ 1st gill-opening	0	11	1	6½
„ anterior edge of pectoral fin	1	3	1	11½
„ anterior edge of ventral fin	2	10¼	4	3
„ base of 1st dorsal fin	3	0	4	7⅜
„ base of 2nd dorsal fin	3	5¾	5	4⅜
Length of pectoral fin	0	8	0	10½
„ dorsal I	0	5	0	8
„ dorsal II	0	4½	0	7

[1] In this paper the description of the brain is by Mr Jackson. The dissection of the fifth group of nerves was made by Mr Clarke, of the eighth by Mr Jackson—and they are severally responsible for the accuracy of the descriptions of these groups. On the other hand, both authors concur in the homologies expressed. The notes on the viscera are extracted partly from the Museum Note-book, and are partly taken from the specimens preserved in the Biological Department.

	Male.		Female.	
Width at eyes	0ft.	7in.	0ft.	9in.
„ spiracle	0	9½	1	1½
Girth behind pectoral	2	0	2	11½
„ in front of pectoral	1	11		
Girth at root of tail	0	8½	1	3½
Length between tip of tail-lobes	1	2½	1	9

Weight of female 250 lbs.

There is no need to give any description of the animal, as Professor Turner has already done so with great care in the May number of this *Journal* (p. 295). In this paper we propose to treat first of the nervous system, which we have been able to work out to a very great extent, and then to append some notes on the visceral anatomy supplementary to those published by Professor Turner in his paper before mentioned. Professor Rolleston has kindly put all the material at our disposal, and has allowed us to extract from the Note-book of the Anatomical Department, aiding us in addition with his counsel and advice, for which we desire to thank him most heartily[1].

§ 1. The cranial cavity in both sharks was very large; and the brain occupied but a very small proportion of it. The cavity continued onwards, surrounding the olfactory tracts. This continuation, as well as the main cavity itself, was filled with a very clear and liquid arachnoid fluid, of a yellowish tint. Strong connective-tissue fibres crossed it in every direction, supporting (apparently) numerous blood-vessels destined for the pia mater.

§ 2. The brains of both individuals disclosed on careful comparison no differences whatever. One—that of the female

[1] The following list gives the titles of the chief works to which we have occasion to refer repeatedly in the course of our paper, and the abbreviations employed for the sake of reference in each case.

Gegenbaur—Ueber die Kopfnerven von Hexanchus (mit Tafel XIII). *Jenaische Zeitschrift*, VI. 1871. (J. Z.)

Gegenbaur—*Untersuchungen zur Vergleichenden Anatomie der Wirbelthiere.* Heft III. 1872. (V. A.)

Von Miklucho-Maclay—*Beiträge zur Vergleichenden Neurologie der Wirbelthiere.* Leipzig, 1870. (M. M.)

Stannius—*Das peripherische Nerven-system der Fische.* Rostock, 1849. (St.)

Henle—*Handbuch der Systematischen Anatomie der Menschen.* Band III. Abtheilung, II. 1871. (H.)

Quain and Sharpey—*Elements of Anatomy*, Vol. II. Ed. 7, 1867. (Q. S.)

Stricker—*Manual of Histology.* Translated by H. Power, M.B., Vol. II. 1872. (Sr.)

Parker—On the Structure and Development of the Skull in the Salmon. *Phil. Trans.* 1873, p. 95. ('Salmon.')

Parker—On the Structure and Development of the Skull in the Pig. *Phil. Trans.* 1874, p. 289. ('Pig.')

—was removed and preserved as a permanent museum preparation, and it is from this specimen that the following description is mainly derived.

The brain of Echinorhinus belongs to the *first type* of Selachian brain described by Miklucho-Maclay. The distinctive marks of this type are according to him (*M. M.* pp. 9 and 10); (i) slight difference in external form between the adult and embryonic brains; (ii) the great permanent size of the cavities; (iii) the longitudinal extent of the adult brain, noticeable especially in the length of the olfactory tracts and the cerebral peduncles; and (iv) the unusual size of the fourth ventricle.

So far as we have been able to ascertain, the brain of this particular shark appears never to have been figured or described. Accordingly the figure (Pl. VII., Fig. 1) has been given, and it is interesting to note the close resemblance existing between the brain of Echinorhinus and the brain of Hexanchus as drawn by M. Maclay (*M. M.* Taf. II. Figs. 8 and 9), and by Gegenbaur (*J. Z.* Taf. XIII. figs. 1 and 3).

§ 3. The olfactory tracts (*Olf.* Pl. VII., fig. 1) are separated by a slight constriction from the succeeding portion of brain. They are long, flattened, and are marked superficially by longitudinal striations. This striation clearly denotes a separation of the fibres into larger and smaller bundles. There is no terminal bulbous expansion: the bundles of fibres simply separate from one another, and spread out like a fan on the posterior surface of the nasal mucous membrane.

The olfactory tracts arise from the anterior angles of the still undifferentiated cerebral lobes and thalami optici. Maclay regards this part of the brain as representing the cerebral lobes alone (Vorderhirn, *M. M.*, p. 2), but there are good reasons for adhering to the ordinarily received nomenclature, as is here done. This portion of the brain is roughly triangular (*C.* Pl. VII., fig. 1) in shape, the truncated apex being turned backwards. The base of the triangle presents at its anterior edge in the middle line a slight furrow, which indicates a commencing differentiation into a right and left lobe. This furrow deepens as it extends on to the inferior surface, where the brain swells out anteriorly on either side into a perfectly distinct elevation. On the upper surface there is a slight indication of similar swellings on either side. But by far the larger portion of the upper surface is occupied by the third ventricle (*V.* 3). To the roof of this ventricle which has been left on the right side is hanging the long filamentary pineal gland (*Pi.*) attached at one end to the roof of the cranium in the natural condition of the parts, and traceable in the membranous roof of the third ventricle back to the *posterior edge* of the third ventricle constituted by the optic lobes. The sides of the third ventricle are but slightly, if at all, thickened, and must be held to represent the little developed optic thalami (*Th.*). On the inferior aspect, and slightly in front of the posterior edge of the third ventricle, rise the optic nerves (*Op.*), small and round, having a chiasma of remarkable lateral extent. Immediately behind the chiasma is the pituitary body—the front portion of which is light-coloured like the rest of the brain—the hind portion (Hæmatosac) dark, vascular and thin-walled. The pituitary body was closely attached to the floor of the cranium.

§ 4. The Mesencephalon (*C. B.*) has but a slight median furrow, but bulges laterally on either side, thus showing the division into a right and left optic lobe. It is partially covered behind by the cerebellum. The inferior surface of this part of the brain is smooth, broad anteriorly, and narrowing somewhat posteriorly. It is slightly depressed in the middle, indicating a separation of a right and left cerebral peduncle. The third pair of nerves (III) arises from it about $\frac{1}{8}$ in. behind the pituitary body by a single root on either side, situate very near the middle line. M. Maclay regards this division of the brain as the Thalamencephalon (= Zwischenhirn).

§ 5. The Cerebellum (Mittelhirn, *M. Maclay*) is lozenge-shaped, and yields to the touch, having without doubt a large internal cavity such as exists in Hexanchus. Anteriorly (*Ce.*) it overlaps the optic lobes, posteriorly the fourth ventricle, both to about the same proportionate extent. It is marked superiorly by a central longitudinal depression, and there are two other slight depressions, one on either side at the external or lateral angles of the lozenge. The slender fourth nerve (IV) arises between the cerebellum and the optic lobes on the upper or dorsal surface.

§ 6. The medulla oblongata (*M. O.*) is of great extent—

making fully one half of the total length of the whole brain. This great length is however obscured partially by the overhanging posterior angle of the cerebellum when the brain is viewed from above. Anteriorly the medulla is broad, about $\frac{3}{4}$ inch; it narrows posteriorly by degrees and passes into the spinal cord, which is barely $\frac{3}{8}$ inch in transverse diameter, and shews a somewhat elliptical figure in cross section.

Forming the floor and sides of the medulla oblongata are four perfectly distinct strands. The outermost (*s.*) is exceedingly slender at its commencement, gradually thickens, and becoming convoluted forms at last the outermost part or free edge of the trigeminal lobes. Internal to this strand is a column (*g*) round and stout from the very beginning. It has five distinct nodular swellings—vagal lobes—ranged one in front of the other. Gegenbaur figures in Hexanchus six of these ganglionic masses. Anteriorly to the first swelling the tract appears somewhat enlarged and curves out of sight, probably joining the outermost tract, and entering into the formation of the trigeminal lobes. Both these tracts seem to spring from the posterior columns of the cord. (*V. A.*, pp. 266 and 267.) Internal to the nodular tract there is another (*p′*) which takes a perfectly straight course—is broad below and narrow above. It appears to correspond chiefly to the lateral column of the cord, and is separated from the tract (*g*) by a well-marked furrow. On its inner side it is separated above and below by an equally well-marked furrow, from the most mesially situated tract of all (*p*), but at about the middle of the medulla this inner furrow is partially obscured by fibres which pass inwards from the tract (*p′*) into the tract (*p*). This latter tract (*p*, anterior pyramid, Gegenbaur, fasciculi teretes, M. Maclay *loc. cit.*) seems to be derived from the anterior column of the cord, is yellowish in colour, and is separated from its fellow by a deep longitudinal fissure (sulcus centralis). It takes also a perfectly straight course fore and aft. In the absence of recent and accurate investigations into the course of fibres from the cord into the medulla oblongata in fish and lower vertebrates, it is safer perhaps not to speculate confidently on the homologies of these several tracts. Judging superficially, the tracts (*p*) seem to correspond best with the anterior pyramids—the tracts (*p′*) with the fasciculi teretes—the tracts (*s*) and (*g*) with the restiform bodies and the fasciculi graciles.

The inferior surface of the medulla is somewhat swollen on either side the middle line. From it rise anteriorly the fifth (V), seventh (VII), and auditory (*au*) nerves. About $\frac{1}{8}$ inch behind the last-named nerve and nearer to the middle line rises the abducens by three rootlets on each side. A quarter of an inch behind the auditory and more laterally placed is the origin of the glossopharyngeal (IX), and the upper (posterior) roots of the vagus (X) issuing from the sides of the medulla in a continuous line as far down as the posterior extremity of the fourth ventricle. On the inferior surface close to one another in the middle line are the lower (anterior) roots of the vagus (X′), four in number.

The roof of the fourth ventricle is exceedingly thin posteriorly. It is thicker in front, and there appears to contain a small quantity of nervous matter, which is at its thickest between the trigeminal lobes.

In discussing the homologies of the cranial nerves we have adopted Mr Parker's views of the visceral arches, embodied in his latest papers on the development of the skull of the Salmon, and Pig, and on the "Form and use of the facial arches" (*Monthly Micr. J.*, 1871, Vol. VI. p. 211).

Hence we consider that the trabeculæ cranii and the palato-pterygoid cartilages constitute two *præ-oral* visceral arches, with a cleft (the lacrymal cleft) between them. (Cp. 'Salmon,' p. 126.)

We have also adopted the view held by Gegenbaur, in his paper on Hexanchus, that each *individual* cranial nerve supplies the anterior and posterior edges of a visceral cleft. By applying these views to the anterior region of the skull, which has undergone considerable change from its simplest condition, it will be seen, in the sequel, that we have arrived at results different to those hitherto attained.

§ 7. The three motor nerves of the eye are all present. They present scarcely anything worthy of note save the fact that the third nerve sends a branch to the external rectus.

As to the homologies of these nerves, whether they are differentiations of the fifth, as held by Gegenbaur, or represent nerves belonging to three suppressed myotomes of Amphioxus, as suggested by Prof. Huxley (*R. Soc. Proc.*, Vol. 23, p. 130), we have no facts to guide us to any further elucidation. The only fact to which we wish to draw attention is this: Gegenbaur (*J. Z.* p. 513) considers it as an important point, that they invariably run below the ramus ophthalmicus: is it not equally important that they are invariably situated above the maxillary branches of the fifth?

§ 8. The roots of the fifth and the seventh are closely connected, as is commonly the case in fishes, therefore it will be as well to describe them together, though the nerves will be treated separately afterwards.

The references are all to Pl. VII. Fig. ii.

Three roots are plainly discernible.

V*a*. The anterior root arises from the inferior surface of the medulla oblongata, by two well-marked rootlets (V*a* 1 and 2) situated one above the other, which join together after about ⅛ inch. The trunk thus formed passes outwards for about an inch, until it reaches the exterior wall of the cartilaginous cranial wall, where it is joined by Vβ.

Vβ. This root has a well-marked superior rootlet, which arises from the lobus trigeminus, and after about ¼ inch joins the inferior rootlet, which arises below from the medulla oblongata in company with Vγ. The nerve thus constituted then unites with V*a* as described above.

Vγ and VII. This root is so closely united with Vβ inferiorly as to be scarcely distinguishable from it. Some of its fibres rise just above the auditory. It becomes closely connected with Vβ, and fibres appear to pass from one to the other.

Thus it will be seen that from the numerous rootlets, two main trunks are formed, which unite, and then differentiate as the Fifth and the Seventh nerves, the latter appearing to be chiefly derived from Vγ.

§ 9. The distribution of the trigeminus is as follows:

Its branches may be divided into those, i. which pass above the orbit (R. ophthalmicus), and ii. those, Rr. maxillares—which pass transversely outwards below the eyeball.

i. The R. ophthalmicus (*Opth.*) divides into the R. ophth. superficialis and the R. ophth. profundus of Stannius. The former

(*Opth.*') of these runs, as is always the case in vertebrata, upwards, closely applied to the posterior wall of the orbit, giving off on its way several small branches (dorsal branches, *d. d.*) to the roof of the skull, which are distributed to the mucous canals and skin. It then pierces the cartilage at the antero-internal angle of the orbit, and is distributed to the skin on the upper surface of the cartilaginous rostrum, from the anterior edge of the orbit forward (*tr*). It is here joined by small branches from the R. ophth. profundus next to be described.

This nerve (*o.n.*) arises from the R. ophth. superficialis, and gives off a long slender twig, the ciliary nerve (*ci.*), which runs forward to the eyeball. After giving off this ciliary nerve, the main trunk passes on under the superior and internal recti and the superior oblique as in man, and piercing the anterior wall of the orbit runs in the substance of the cartilage underneath the branches of the superficialis. With this nerve it anastomoses, as has been mentioned above, and has a similar distribution (*tr.*).

Gegenbaur (*J. Z.* pp. 508, 545, et seq.) identifies the R. ophthalmicus with the R. dorsalis of a spinal nerve, a view we also put forward in the *Academy*, May 29, 1875, p. 561. The following considerations, however, have led us to change our opinion.

In all vertebrata the Ophth. superficialis is constantly present, and invariably lies above the eye close to the ethmoidal region, and it commonly sends branches forward to the pituitary membrane of the nose, and even as far as the termination of the face above the premaxillary. In this shark it is distributed *above* the rostrum, and so also is the profundus. The rostrum, be it remembered, is a development of the trabeculæ cranii.

It has been sufficiently proved that the trabeculæ cranii are the first pair of præ-oral visceral arches, often perfectly independent of the investing mass with which they subsequently unite (cf. 'Pig,' p. 327, Pl. XXVIII. Figs. ii. and v. *tr.*; 'Salmon,' p. 122, Pl. I. Fig. v. Pl. II. Fig. v. *tr.*). The direction of their long axis, however, has undergone a change: the distal ends rotating upwards and forwards, consequently the primordial anterior surface has become continuous with the dorsal aspect of the body, though homologically it is *not* a *dorsal* surface. Hence the R. ophthalmicus is a nerve distributed to the anterior edge of a visceral arch (viz. the trabeculæ cranii), as may be concluded from the description given above. Accordingly we regard this nerve as the *prætrabecular nerve;* a position strengthened by the fact that Prof. Huxley describes a nerve in Amphioxus running above the eyespot, and parallel with the chorda dorsalis, which he states "has the characteristic course and distribution of the orbito-nasal division of the trigeminal" (*loc. cit.* p. 130). If any branches are to be regarded as rami dorsales, they must be those we have lettered *d. d.*

As to the special homologies of these branches, the superficialis has in fish, reptiles and birds an extensive distribution, whereas in man it has become restricted to 'frontal' branches. The profundus, on the other hand, appears, from its relations to the muscles of the eye, and its distribution, to correspond with the nasal branch of the ophthalmic division of the fifth. The branches *d. d.* in Teleostei become intra-cranial branches, and in man probably correspond to the nervus recurrens ophthalmici of Arnold, which goes to the dura mater (*H.* p. 354).

ii. The branches below the eyeball are the superior and inferior maxillary nerves. After the R. ophthalmicus has been differentiated from the fifth, and before the trunk divides into these two nerves just mentioned, two or three small branches (*d′ d′*) arise, which pass upwards and outwards through the cartilage, and are distributed to the skin above and behind the orbit.

The nerve then divides into two trunks.

The upper of these, the superior maxillary (*mx.*), divides into three branches, an anterior branch (*n. p.*), which is by far the stoutest of the three, and turns over the anterior edge of the palato-pterygoid. It then courses along below the rostrum (trabeculæ cranii) on the inner side of the nose, supplying this part of the skin with sensory branches.

Of the two other branches, one (*I. O.*) arises from the upper part of the nerve, is exceedingly slender, and is distributed to the skin on the inner side and below the orbit, in front of the labial cartilages. The other (*s. pa.*), somewhat larger, is distributed along the outer or anterior edge of the palato-pterygoid cartilage in its whole extent; it gives a twig (*m*) to a small cylindrical muscle, which lies behind the labial cartilages, and extends between the inferior edge of the orbit and the external angle of the mouth. All the other branches of this nerve (*s. pa.*) are distributed to the skin between the labial cartilages and the pterygo-palatine bar.

The second of the two trunks (*mn.*) into which the fifth divides (*supra*), gives off first a slender branch (*b*), which is distributed to the skin behind the orbit, and above the labial cartilages—a spot to which pass also a few other fine twigs from the main trunk. It then curves over the palato-pterygoid cartilage, giving off (i.) a small fine twig (*au*) to a muscle connecting the palato-pterygoid cartilage to the auditory capsule; (ii.) a stouter branch (*P. M.*) to a large muscle passing from the outer end of the palato-pterygoid bar to the upper end of Meckel's cartilage or the mandible. The main stem of the nerve (*mn'*) curves round the angle of the mouth, and runs along the outer surface of the mandible, distributing branches to the skin and edge of the jaw.

Gegenbaur in his paper on Hexanchus, and his work on the Vertebrata (*V. A.* p. 228, et seq.) regards the labial cartilages as visceral arches. It is more than doubtful whether this is a tenable view. On the other hand, he does not regard the palato-pterygoid as a visceral arch at all, whereas it has undoubtedly been shown to be so by Mr Parker's researches (cf. 'Salmon,' pp. 141, 126, Pl. I. Figs. i. and vii. *pa*; Pl. II. Figs. iii. iv. *p. pg.*; 'Pig,' p. 327, Pl. XXVIII. Figs. ii. v. *p. pg.*). He regards the nerves accordingly as not related to the pterygo-palatine, but to the labial cartilages.

A careful consideration of the superior maxillary in Echinorhinus has led us to regard it as the nerve supplying the posterior margin of the trabecular arch, and the anterior edge of the palato-pterygoid. The cleft between them, the lacrymal cleft, is not persistent in fishes, save perhaps in the Dipnoi, though it exists in the higher vertebrata.

The nerve (*n. p.*) runs along the inferior surface of the trabeculæ, which it has been previously shown (*supra*) must be homologous with the posterior margin of that arch. It is also internally placed to the nose and the eye, and consequently would be the nerve in front of the lacrymal cleft. This cleft is regarded by Mr Parker ('Pig,' p. 328) as representing externally the lacrymal duct, internally the posterior nares. The only nerve with which it can be homologous in the higher vertebrata is therefore the naso-palatine, which is distributed along the mesethmoidal cartilage, a development of the trabeculæ cranii.

The nerve (*s. pa.*) on the other hand is distributed along the whole of the edge of the pterygo-palatine. Its branches lie between the labial cartilages and the second præ-oral visceral arch, in relation with its anterior margin; they must therefore be post-lacrymal nerves, and consequently are to be regarded as supplying the anterior margin of the second præ-oral arch. Supposing the labial cartilages, which are most probably the foundations (so to speak) of the premaxillary and maxillary bones of the higher vertebrata (cf. Gegenbaur, *Grundz.* 1870, p. 645), were more developed, they would necessarily, from the mode in which the branches of this nerve are distributed, enclose it completely between themselves and the palatine arch. This is precisely the relation held in man by the spheno-palatine nerves, which are often independent of the spheno-palatine ganglion (*Q. S.* p. 603 and *H.* p. 377), and which, where the premaxillaries, the maxillaries, and the palatine bones do not develop palatal processes, are situated externally to the internal nares,—the inner extremity of the lacrymal cleft.

The nerve (*I. O.*) appears to be a branch of (*s. pa.*) distributed below and to the inner side of the orbit; its inner fibres are distributed to the same spot as the inner fibres of the nerve (*s. pa.*): its outer fibres lie between the orbit and the labial cartilages, and would therefore lie externally to them, supposing they were more developed; it appears therefore to correspond best to the infra-orbital of man, and to the nerve in Hexanchus and Squatina, which is identified as infra-orbital by Gegenbaur (*J. Z.* pp. 508—511).

As to the inferior maxillary nerve, the prolongation (*mn'*) along the Meckelian cartilage is no doubt homologous with the lingualis and the inferior dental. It is the nerve which runs behind the oral cleft, and supplies the anterior margin of

Meckel's cartilage. As Meckel's cartilage is the third visceral arch (the first post-oral), we ought to have a branch of the inferior maxillary nerve distributed in front of the oral cleft, and to the posterior margin of the palato-pterygoid cartilage. As a matter of fact there is a præ-oral branch of the infra-maxillary, the nerve (*b*), which inasmuch as it is distributed behind the eye, above the mouth and labial cartilages, and in front of the articulation of the mandible, corresponds most nearly, if to any, to the buccal branch of the infra-maxillary nerve in other vertebrata. But this nerve, though it is præ-oral, has lost all connection with the palato-pterygoid arch, and the posterior margin of that arch is supplied not by the fifth, but by the palatine branch of the facial (*vide infra*, § 10). This appears to be a somewhat startling difficulty, but it is a difficulty which disappears when we consider the changes of direction and growth which the palato-pterygoid arch undergoes. Instead of retaining its normal direction, more or less parallel with the course of the nerves, and of the arches in front and behind it, it has come to be placed more or less transversely to its original axis. Further, its posterior or upper extremity grows in the fish in such a manner as to become hooked on to the first post-oral arch, but as the direction of growth is *not external* to the præ-oral branch of the infra-maxillary, but *internal* to it, the palato-pterygoid comes to receive, what may be termed, for want of a better phrase, an adventitious nerve-supply from the seventh.

As to the dorsal branches of the nerve, before it divides into inframaxillary and supramaxillary, they seem most nearly to represent the nervi recurrentes of Arnold (*H.* pp. 367 and 381). In Teleostei they are represented by the intra-cranial branches (*St.* p. 47). Perhaps some of their branches, which stretch far out behind the orbit, at a level with the angle of the mouth, may be homologous with the auriculo-temporal. To sum up, the trigeminus appears to consist of three distinct nerves :

(i.) A prætrabecular nerve—the ophthalmic:

(ii.) A præpalatine nerve (supramaxillary), which divides into an anterior or præ-lacrymal branch (naso-palatine), and a posterior or post-lacrymal branch (spheno-palatine and infra-orbital).

(iii.) A præ-Meckelian nerve (inframaxillary), which divides into a præ-oral branch (buccal ?), and a post-oral (lingualis, and inf. dental).

§ 10. It remains now to discuss the distribution of the seventh nerve (VII). This nerve gives off one or two fine twigs (*d″*), which run upwards in the cartilage to the surface of the skull: these are Rami dorsales, and appear, so far as can be ascertained, never to have been discovered previously. The nerve then gives off a stout branch forwards, but just at its origin this branch gives off two or three fine nerves, which run between the rudimentary branchiostegal rays of the spiracle and the mucous membrane, which is thrown into folds: these are the præspiracular nerves (*Sp.*).

The rest of the branch runs on, and breaks up into numerous twigs (*pt.*), distributed to the mucous membrane of the mouth, and to the teeth of the palato-pterygoid cartilage. The main trunk of the facial running along the hyomandibular behind the spiracle distributes nerves (*h. br.*) to the muscles in front of the branchiostegal rays of the hyoidean arch, and to the skin; also a branch (*an*) forward to the skin, at the articulation of the mandible with the palato-pterygoid, a region also supplied by some of the dorsal branches of the trigeminus. It then divides into two branches, the R. mandibularis externus and the R. mandibularis internus of Stannius. The latter of these nerves (*ch*) runs above the ligament connecting the upper end of the mandible with the upper end of the hyoid; it is distributed to the mucous membrane between the hyoid and the mandible, as well as to the teeth on the posterior surface of that visceral arch. The former, or external mandibular branch, runs along the outer surface of the hyoid to the middle line, and distributes branches to the skin, and to the thin flat muscle which lies between the two diverging rami of the mandible, extending also far backwards (*F*).

It will thus be seen that the facial divides into a præ-spiracular and a post-spiracular nerve, but the branch from which the præ-spiracular nerves are given off is distributed also to the mucous membrane of the mouth. We here meet for the first time with a ramus pharyngeus destined for the walls of the digestive tract. This ramus pharyngeus, identified as such by

Gegenbaur (*J. Z.* p. 524), is the palatine nerve of Teleostei. In those osseous fishes it becomes connected with the superior maxillary nerve, supplies sensory branches to the palato-pterygoid arch, and to muscles which draw the palatal apparatus to the base of the skull, as in Perca and Gadus. In Teleostei, therefore, it may be both sensory and motor: in the Sharks, on the other hand, it appears to be entirely sensory. On this ground Gegenbaur objects to its homology with the great superficial petrosal of Mammalia, because in Mammalia experimentation shows that intracranial section of the facial paralyses the muscular branches to the soft palate, which are known to be derived from the great superficial petrosal. On the contrary, it may be urged, that the facts adduced by Hermann (*Grundriss*, Ed. 4, pp. 316, 317), as well as the arguments long ago urged by Mr Lewes (*Nat. Hist. Rev.* I. 176), clearly indicate that to determine the homology of a nerve by reference to its function is exceedingly dangerous.

In the frog it is stated that the facial nerve is entirely sensory, but no one for that reason doubts its homology with the facial of man, which is generally considered as entirely motor. In the Shark there are no muscles developed in the mucous membrane behind the palato-pterygoid, hence the nerve *cannot* be motor. In the Teleostei, already alluded to, there are such muscles, and they are supplied by the palatine nerve (cf. *St.* p. 56). Similarly the velum pendulum palati is muscular, and the branches of the seventh, which are distributed to it, are accordingly motor. Hence the purely sensory nature of the palatine in the Shark is *no* argument against its homology with the petrosal nerves. On the other hand, it may be urged from morphology, that the relation of the great superficial petrosal to the inner end of the spiracle or Eustachian tube, is such as warrants us in considering its homology with the palatine nerve as all but certain. The pharyngeal branch of the spheno-palatine ganglion (*Q. S.* p. 605) is frequently derived altogether from the vidian, and it is a sensory nerve. Perhaps it may be represented by the præ-spiracular nerve in part[1]. Another argument in favour of the homology between the pala-

[1] A nerve which becomes greatly reduced when the spiracle is small or obsolete.

tine nerve in Elasmobranchs and the great superficial petrosal, is that they both spring from a ganglion, the geniculate ganglion (cf. *St.* p. 55). It is possible that the palatine nerve represents both the petrosal nerves, as in the Sturgeon it is connected with the glosso-pharyngeal (vide infra § 12).

The Ramus mandibularis internus (*ch*), from the course it takes over the ligament connecting the mandible to the hyoid, is evidently homologous with the chorda tympani, while the Ramus mandibularis externus (*F.*) as evidently corresponds to the main trunk of the facial in Mammalia, from its close connection to the hyoid.

With reference to a point already discussed, viz. the curious relation subsisting between the palatine nerve and the posterior margin of the palato-pterygoid cartilage, it is as well to note the fact, that the post-spiracular nerve by means of its branch (*ch*) supplies the posterior margin of the Meckelian arch, whereas the nerve-supply ought to be derived from the præ-spiracular. This change is no doubt due to the secondary connections established between the first and second post-oral arches, just as in the former case it was argued that the change was due to a similar secondary connection established between the second præ-oral arch and the first post-oral.

§ 11. The auditory nerve rises by a large root inferiorly placed to the root Vγ and VII, and it appears to have no connection whatever with that root. It divides into three primary branches:

(i.) To anterior vertical semicircular canal (ampulla).

(ii.) To vestibule, etc.

(iii.) To ampulla of posterior-vertical semicircular canal.

Gegenbaur, in his paper on Hexanchus (*J. Z.* p. 545), and in his work on the Vertebrata (*V. A.* pp. 283 to 285), has broached the theory that the auditory is the long-missing Ramus dorsalis of the facial. In our shark, a Ramus dorsalis has been found, and hence it might be said that Gegenbaur's view is untenable. This is *not* necessarily the cause, because the auditory might still be a branch of the R. dorsalis. Meynert contends strongly for the view that the auditory "belongs to a different category from the other nerve-roots," from its anatomical connections with the cerebellum (*Sr.* Vol. II. p. 500). Perhaps investigations on the nuclei of origin of the auditory nerve in the lower Vertebrata might throw additional light on this obscure and puzzling question.

The fifth group of nerves quits the cranium in front of the auditory capsule. The next group, the eighth, consisting of the Glosso-pharyngeal and Vagus nerves, passes out below and behind it. The former is a single nerve, comparable to the seventh, as is shewn by its distribution to a single visceral arch, while the latter shows markedly its compound nature both in its roots and its distribution to more than one arch.

The references are to Pl. VII. Fig. iii.

§ 12. The Glosso-pharyngeal nerve (*Gp.*) arises from the side of the medulla oblongata. Its single root—a stout bundle of fibres—is situated about ¼ inch behind the root of the auditory nerve, and lies immediately below, or ventrally to, the first strand of the upper (*i.e.* posterior) roots of the vagus, and in consequence is completely concealed by that nerve when the brain is viewed from above. The two nerves here appear as in Teleostei to be more closely apposed than they are in Hexanchus (cf. *J. Z.* VI. Taf. XIII. Fig. iii. *Gp.*, and *M. M.* Taf. II. Figs. 8*a* and 9). A careful examination failed to detect any interchange of fibres at this point between the roots of these nerves.

The nerve-trunk runs obliquely backwards, at an angle with the medulla less acute than that formed by the vagus, and enters a canal in the cartilage. The course of this canal and its contained nerve is then as follows. It dips obliquely downward below the ampulla of the posterior semicircular canal of the ear, and then turns horizontally outwards and backwards. The external opening of the canal is somewhat trumpet-shaped, and lies at the level of the upper extremity of the first branchial slit. While in the canal the trunk of the glossopharyngeus is somewhat swollen, and when fresh of a yellowish colour, due probably to the presence of ganglionic elements. No communication of this nerve with the sympathetic was observed (cf. *St.* p. 76).

A small nerve (*d*), observed by Stannius in Spinax and Carcharias (p. 79), and by Gegenbaur in Hexanchus (p. 517), quits the glossopharyngeus while still in its canal. This *Ramus dorsalis* runs outwards and upwards through the cartilage in a special canal, and is lost on the superior surface of the cranium in the neighbourhood of the mucous canal. In man it is probably represented by the branch to the auricular nerve. Another small nerve (*d**) leaves the main trunk at the same point as the R. dorsalis, and running on in the main canal, is apparently lost in the upper part of a muscle connecting the suspensorium to the cranium.

The main trunk of the glossopharyngeus then divides into two branches, the Ramus anterior s. hyoideus, and the R. arcus branchialis primi (Stannius), which respectively supply, one the front, the other the hind, wall of the first branchial slit.

i. The anterior or hyoidean branch (*br.*), present in all Elasmobranchs and Ganoids (probably), variable in Teleostei, gives off close to its origin a visceral nerve, the R. pharyngeus (*Ph.*), homologous with the palatine branch of the facial and the Rr. pharyngei of the branchial nerves derived from the vagus.

This R. pharyngeus is rarely present in Teleostei. In the Carps it supplies their peculiar erectile organ. In Elasmobranchs it is distributed to the mucous membrane of the roof of the mouth, running forwards behind the spiracle, and in Accipenser it anastomoses with the palatine nerve, and then reaches as far forwards as the superior maxillary nerve. This course and anastomosis render its homology probable in the higher vertebrates with the tympanic or Jacobson's nerve, the connection of which with the small superficial petrosal is thus explained.

The *anterior* branch lies behind the branchiostegal rays of the hyoid, and divides into several twigs, the innermost supplying the mucous membrane of the inner surface of the hyoid, and in Spinax (*St.* p. 78) uniting with filaments of the facial. The outermost twigs are *here* in relation with the anterior gill-lamina of the anterior gill-pouch: in Accipenser they supply the opercular gill, and in Teleostei, which possess a pseudobranchia, a few filaments run to that organ. This anterior branch probably constitutes the main trunk of the nerve in the higher vertebrata, which is closely related to the anterior cornu of the hyoid.

ii. The *posterior* branch (*br'.*), or nerve of the first branchial arch, is apparently present in all fish. It is distributed to the musculature of the first branchial arch, to its mucous membrane, and the posterior gill-lamina of the first gill-pouch. According to Stannius (p. 79) some of its fibres are prolonged to the floor of the pharynx. In higher vertebrata, which have lost this gill-slit (second post-oral), this branch is possibly represented by the branches of the glossopharyngeal which unite with branches of the vagus to form the pharyngeal plexus.

The glossopharyngeal, of all the cranial nerves, best accords with the type of the spinal nerves. It is a mixed nerve, motor and sensory (cf. *St.* p. 75), and possesses a dorsal branch, a ventral branch, which gives off a nerve to the digestive tract, and divides into an anterior and a posterior branch in relation with the anterior and posterior margins of a gill-slit.

§ 13. The Vagus has, as in Hexanchus, Spinax, and Carcharias, both upper (posterior) and lower (anterior) roots. As the nerve-trunks formed by the union of these two sets of roots are in this shark distributed in very different ways, it will be as well to describe and discuss them separately.

The upper or posterior roots (*Vg*) appear to be connected with the ganglionic swellings mentioned (§ 6), in the medulla. They rise from the medulla in a continuous row—the hindmost roots as low down as the point at which the side walls of the fourth ventricle unite. They diminish as in Hexanchus (cf. the figures before alluded to) in size from before backwards, and the posterior strands turn obliquely forward to unite with the main trunk. The number of roots is not constant in both specimens, nor on both sides of the same specimen, varying from six to eight in number. They, however, unite more or less clearly into five trunks, which in their turn coalesce to form the vagus nerve. The roots show superficially fine longitudinal striations, indicating their component bundles of fibres.

The right vagus is slightly larger than the left. On each side the nerve turns obliquely backwards and enters a funnel-shaped canal in the cartilage which runs behind the arch of the posterior vertical semicircular canal. The internal opening of this canal is about one inch behind the internal opening of the canal for the glossopharyngeus. The trunk of the nerve while yet within the canal becomes of a yellowish hue, differing from the white tint of the rest of the trunk, and due probably to the presence of ganglionic elements; but it can scarcely be said to enlarge appreciably.

The nerve then divides into rami dorsales (and ramus lateralis) and the truncus branchio-intestinalis.

§ 14. The ramus dorsalis and the lateral line nerve are of special interest; the latter probably representing a number of rami dorsales united into a single trunk.

From the trunk of the vagus, still in its canal, there springs on each side a slender nerve, R. dorsalis (d'), which runs in a special canal of its own upward to the skin on the surface of the head. This nerve is present in Hexanchus, wanting apparently in other sharks, and probably corresponds (Gegenbaur) in the Teleostei to the branch which runs upwards inside the cranial cavity, and is present wherever a corresponding branch is developed from the trigeminus, or where a ramus lateralis trigemini is given off by the same nerve, with which this R. dorsalis unites. At the same spot in Echinorhinus, from which this R. dorsalis springs, there arise on the right side two, on the left three nerves (d''), which pierce the cartilage at short distances from one another, and then emerging run outwards along the fibrous septum which stretches down the sides of the body, separating the upper lateral from the lower lateral muscles. The nerves in question are distributed to the very edge of this septum, probably to the mucous canal, and the most anterior of them reaches that canal just *in front of the first branchial slit.* On the right side the most posterior of these branches anastomosed with a nerve given off from the lateral line nerve further down. These nerves probably correspond to the opercular branch of the lateral line nerve in Teleostei, which, as Stannius (p. 110) pointed out long ago, is homologous with the auricular nerve in the Mammalia.

All these nerves arise from the anterior margin of the trunk of the vagus. This portion of the trunk begins to show signs of separation at the spot where the vagus passes out of its canal, and finally separates entirely after the third branchial nerve has branched off, and becomes the lateral line nerve (*L.*). This important nerve runs along the fibrous septum (mentioned above), and from its outer margin pass off numerous twigs, distributed apparently to the mucous canal. No connection between this lateral line nerve of the vagus and the spinal nerves was observed—a point in which, according to Stannius (p. 96), it differs entirely from the ramus lateralis of the trigeminus, where such a connection always takes place.

Is the nerve of the lateral line serially homologous with a ramus dorsalis? Is it one R. dorsalis, or does it represent a number of rami dorsales fused? In his paper on Hexanchus Gegenbaur (p. 541) argues against the homology of the lateral line nerve with a R. dorsalis, on the ground that its distribution passes beyond the distribution of the rest of the vagus. The R. dorsalis, he says, must be restricted to the occipital region of the skull, into which are fused the vertebral segments to which the vagus corresponds. This argument must not count for much, because *no* similar objection can possibly lie against the homology of the R. lateralis of the trigeminus with a R. dorsalis (cf. *St.* p. 49, pp. 51—54). Yet certainly this nerve has also passed beyond its proper territory. Gegenbaur, however, in his work on the vertebrata before alluded to (p. 280), appears to regard the homology in question with a more favourable consideration—a conclusion to which he is led by the apparent correspondence of the R. intestinalis to a number of Rr. ventrales.

The arguments in favour of regarding the lateral line nerve as homologous with a R. dorsalis may be briefly summed as follows:

(i.) It shows in Echinorhinus early traces of a separation from the main trunk of the nerve. It is evidently continuous with that part of the vagus from which the R. dorsalis of Gegenbaur arises.

(ii.) There are present in the same shark two or three intermediate nerves, which are derived from the differentiating lateral line nerve close to the R. dorsalis, pierce the cranial cartilage, and are distributed to the edge of a fibrous septum that extends down the body, dividing the superior lateral masses of muscle from the inferior. A mucous canal exists at the edge of this fibrous septum.

(iii.) The lateral line nerve itself lies on this same septum, and its branches pass outwards to the edge in the same manner as do the nerves mentioned (ii. *supra*), and on one side of the body there exists an anastomosis with the hindermost of these nerves. Consequently we have here a gradation from the R. dorsalis into the lateral line nerve and its branches.

(iv.) Gegenbaur maintains, and there can be no reasonable doubt of his being right, that each branchial nerve derived from the vagus is the morphological equivalent of a single spinal nerve, or of such cranial nerves as the facial and glossopharyngeus. It is a striking fact that in Hexanchus (*J. Z.* VI. p. 524) the first branchial nerve is to all intents and purposes a distinct and separate nerve. The spinal nerves, the glossopharyngeus, and in this shark the facial, have each their Ramus dorsalis.

Now, unless we may regard the lateral line nerve as representing a R. dorsalis, we *must* suppose that the spinal nerves, which have fused to form the vagus, *retain* their Rr. ventrales (= Rr. branchiales), but have, on the contrary, *lost* every trace of their Rr. dorsales; a supposition at once unnecessary and improbable.

It is exceedingly likely, furthermore, that the lateral line nerve represents a number of Rr. dorsales, because:

(i.) It has so extensive a distribution (*V. A.* p. 280).

(ii.) There are in Hexanchus at least five branchial nerves (in Heptanchus six?) known to us which have lost their Rr. dorsales. Further, the R. intestinalis represents without doubt a number of Rr. ventrales—a number which is not known to us, and these Rr. ventrales imply in their turn the existence of corresponding Rr. dorsales.

Why the lateral line nerve with such an origin has acquired a distribution so extensive, and how this distribution originated, are difficult questions impossible to answer. But precisely similar difficulties attach to the R. lateralis nervi trigemini—an undoubted dorsal branch with a distribution greatly extended beyond the normal.

§ 15. The truncus branchio-intestinalis, the second great branch into which the vagus divides, is an exceedingly stout nerve. It gives off four branchial nerves before finally passing to the heart and stomach.

Of these branchial nerves the three first (*Br.* I. II. III.) are exact repetitions of the glossopharyngeus, and are related in a similar way to visceral arches and clefts. The only points to note are that the R. pharyngeus (*ph'*) arises indifferently from the anterior (*a*) or posterior (*p*) division, but that the muscular branches appear to be derived invariably from the posterior division of the nerve.

The fourth branchial nerve (*B.* IV.) differs somewhat from the three foregoing, a difference due to morphological change in its arch. It rises from the vagal trunk beyond the spot where the lateral line nerve has become completely differentiated. The anterior (*a*) division is a stout branch distributed as usual, but it furnishes in addition a small twig (*m'*) to the muscle at the top of the arch (IVth) and a slender pharyngeal branch (*ph'*). The posterior branchial division (*p*) or nerve of the Vth arch has become changed. At the spot where the main branch splits into the anterior and posterior nerves, the latter gives off a fine long nerve (*m''*), which is distributed to a muscle connected below to the front edge of the epicoracoid, above to the anterior margin of a large muscle arising from the exoccipital region of the skull and attached to the supra- and præscapular regions of the shoulder-girdle. The posterior branchial division then passes on, distributing a few fine filaments (*v*) to mucous membrane and muscle clothing the anterior surface of Vth arch, and finally (*ph''*) turns round the posterior margin of the arch on its way to the pharynx. It has a branch of anastomosis (*an.*) with the first visceral or intestinal nerve.

Immediately after the fourth branchial nerve is given off, there arises from the trunk of the vagus a nerve (*m'''*), which is connected by a short and remarkable anastomosis with the cervical cord (*vide infra*, § 16), and is distributed to the outer part of the same muscle as *m''* (*supra*).

The trunk of the vagus from which several fine nerves (*œ*) pass off inwards, apparently to the œsophagus, then resolves itself into the main intestinal branches (*I*), which subdivide several times, and turning over the margin of the Vth (aborted) arch, pass to the viscera (œsophagus, stomach, heart, &c.). These nerves, however, were not traced to their ultimate distribution.

The transition state of the fourth branchial nerve is interesting. It becomes the first R. pharyngeus inferior of Teleostei—a nerve which sends forward a twig, the R. anterior, to be distributed to the hind margin of the fourth branchial arch. This twig is small, or wanting, in Fish (*e.g.* Cyclopterus), where the IVth arch carries only a single row of branchial filaments. The main stem of the R. pharyngeus inferior encircles the œsophagus. Here the posterior ramus of the branchial nerve has a much reduced muscular branch, its main stem *is* pharyngeal. It is thus on the high road to becoming exclusively an intestinal branch. This is precisely what must have happened to the Vth branchial nerve of Hexanchus, which is not represented in Echinorhinus as a distinct branchial nerve at all. Gegenbaur (*V. A.* p. 279) considers it probable that the intestinal branches represent a number (unknown) of branchial nerves which have become restricted to a visceral distribution simply through the suppression or transitory nature of their visceral arches and clefts. This is exceedingly likely, for though the slit and arch disappear, the wall of the pharynx remains, but remains unbroken. It can therefore be scarcely supposed that the nerves of the arches, which are essentially only thickenings in the walls of the pharynx, have disappeared *in toto.* In the Abranchiate vertebrates the process of reduction has been carried to an extreme—the branchial nerves are represented *only* by intestinal branches, showing no trace of their original form. The change is due simply to changes of growth and development. When an air-bladder is present in Fishes it has its nervous supply from the vagus, because it is an outgrowth of that part of the tract which is supplied by the vagus. So, too, the trachea, larynx and lungs of pulmonate vertebrates are supplied by the vagus. Here nerves, which attain a great development, are engrafted on the original vagus, in obedience to a change of growth and development—a change of precisely the opposite character to that undergone by the branchial arches and slits.

§ 16. In Echinorhinus there appear to be four inferior or anterior roots (*Vg.*) of the vagus, increasing in size from before backwards. Hexanchus has "three to four pair," and in Spinax and Carcharias there are, according to Stannius (p. 83), a pair of anterior roots. But the distribution of these roots in Echinorhinus, as the sequel will show, is entirely different to what it is in the three other Sharks named. The number was the same in *both* our specimens.

The first (*Vg.* I.) is a very slender and fine nerve rising from the anterior or inferior surface of the medulla oblongata, nearly half an inch above the posterior limit of the fourth ventricle. It runs backwards at a sharper angle with the medulla than do the posterior vagal roots, and enters a long canal in the exoccipital (?) cartilage, divides into two or three fine filaments, and is distributed to the upper part of the long muscle which, springing from the exoccipital region of the skull, is inserted into the supra- and præ-scapular regions of the shoulder-girdle. This nerve is torn away from the brain, which we have figured, but it was found in the skull.

The second root (*Vg.* II.), a stouter nerve, rises about a quarter of an inch behind the first, and enters a special canal in the cartilage. The third nerve (*Vg.* III.) rises nearly at the same distance behind the second, and the fourth (*Vg.* IV.), which has a double root, at the same distance behind the third, and both likewise enter special canals in the cartilage. These three nerves each give a twig (d'') laterally into the muscle already mentioned, but the chief part of their fibres (v') pass on and join the cervical cord, which is also partly constituted by the four first spinal nerves.

The first spinal nerve (*Sp.* I.) rises about an inch behind the posterior extremity of the fourth ventricle. The posterior root (P) on each side is a fine slender nerve which passes obliquely backwards for some distance in the spinal canal, then pierces the cartilage, and forms a ganglion. The anterior root (A) has two rootlets, and springs from the cord about $\frac{3}{8}$ inch behind the fourth (anterior) vagal nerve, and somewhat in front of its dorsal root. It passes back similarly some way in the spinal canal, and then through the cartilage about $\frac{5}{16}$ inch behind the canal for the last anterior root of the vagus. The nerve then bifurcates—one branch (*as*) runs upwards to the ganglion of the posterior root which it joins, the other branch (v'') joins the anterior vagal nerves. From the ganglion there are branches (*ds*) which pass into the muscle, and another fine twig (*ps*) which passes down and joins the second of the strands into which the anterior root divided, constituting the anterior primary branch. A kind of triangle is thus formed, very similar to Stannius' figure of the ganglion and roots in the Sturgeon (*St.* Taf. IV. Fig. 5).

All the following spinal nerves arise in the same manner, only their roots pass out directly instead of running a long way within the spinal canal. The anterior root invariably has three or four rootlets, and is situated in front of its corresponding posterior root.

The anterior primary branches (*Sp.* II. III. IV.) of the three spinal nerves (after the first) join the first and the three last vagal roots at once, to constitute the cervical cord. This cervical cord gives off a small twig (*an'*) which unites with the muscular nerve of the vagus (cf. § 15 *m'''*), and then receives the anterior primary branch of the fifth spinal nerve (*Sp.* V.). It then divides into two branches which are distributed as follows.

The first, or more externally placed (*Cv*), is the stouter of the two branches. It runs down closely applied to the præcoracoidal region of the shoulder-girdle, gives off two small branches and then passes through a foramen at the base of the epicoracoid, and, coming out on the ventral surface, is distributed to the muscles of the pectoral fin. The second division (*Cv'*) runs behind the rudimentary Vth arch, and then breaks up, some of the twigs going to the muscular (?) membrane which connects the Vth branchial arch to the epicoracoid, and supplying it in conjunction with one of the small branches given off by the first division before entering the foramen. The second of the small branches derived from the first division, in conjunction with the remaining branches of the second division, are lost in the ventral muscles which have their attachment to the posterior edge of the epicoracoid.

In the distribution of the anterior vagal roots, and in the union of the three last with the five first spinal nerves, Echinorhinus differs completely from Hexanchus, Spinax and Carcharias, according to the descriptions given by Gegenbaur and Stannius respectively. It might be urged that because the anterior vagal roots in the three Sharks just named unite with the trunk formed by the union of the posterior vagal roots outside the skull, but here in Echinorhinus unite, not with the posterior roots of the vagus, but with spinal nerves; they are therefore not anterior vagal roots, but anterior roots of spinal nerves which have lost their posterior roots.

The answer to this objection, which is *primâ facie* a good one, lies apparently in the following facts.

i. The foremost of these anterior vagal roots arise from the medulla oblongata some way above the posterior extremity of the fourth ventricle. Consequently the posterior vagal roots extending backwards to the very extremity of the fourth ventricle, extend also far behind the place of origin of the anterior vagal roots mentioned. Hence we must either admit that the roots in question are the anterior roots of spinal nerves *shifted* far forwards and *deprived* of their posterior roots, or else allow that they represent anterior roots corresponding to posterior roots actually present and represented by the upper roots of the vagus. The former supposition seems both gratuitous and absurd; and the mode and place of origin of these nerves clearly point to their connection with the vagus.

ii. The first anterior vagal root remains independent. It does not unite with spinal nerves, and it enters a muscle which connects the upper part of the shoulder-girdle to the skull. In Spinax (*St.* p. 83) branches from the main trunk of the vagus enter this same muscle, and in Cottus (*St.* p. 122) a branch from a nerve, regarded by Stannius as the first spinal nerve wanting the posterior root, enters the homologous muscle.

iii. Though it is true that the three posterior vagal roots unite with spinal nerves, it must be remembered that each sends a twig into the muscle into which the first anterior vagal root enters exclusively, and also that the nerve-trunk, formed by the conjoined anterior vagal roots and first spinal nerves, is in close connection with a branch of the vagus by the branch of anastomosis mentioned before (*supra*, § 15). Accordingly, in spite of the union of the anterior vagal roots with spinal nerves, it is possible that they have not lost their connection with the posterior roots.

It is also a remarkable fact, and one worth noting, that in Teleostei branches derived from the Rr. pharyngei inferiores are distributed to the muscular floor connecting the ventral ends of the branchial arches and the ossa pharyngea inferiora to the shoulder-girdle (*St.* p. 90). In the Sharks (*St.* p. 122) the same parts are supplied by the two first spinal nerves. Here in Echinorhinus they are supplied by conjoined vagus and spinal nerves (see *ante*, *Cv'*).

An interesting point of inquiry in connection with the vagus is the relation of the hypoglossus and accessorius Willisii of Mammalia and Sauropsida to these anterior roots of the vagus. Gegenbaur, in his paper on Hexanchus, so often referred to already, derives the hypoglossus from the anterior vagal roots. The spinal accessory, he says, "is obviously represented by the posterior part of the upper (*i. e.* posterior) row of roots of the vagus—it is still a part of the vagus itself" (*J. Z.* p. 530). This homology is somewhat doubtful.

In the first place, according to Meynert (*Sr.* pp. 524—5), the roots of both hypoglossus and spinal accessory are connected with masses of grey matter in the medulla oblongata, which in the cord correspond respectively to the inner portion of the anterior grey cornu, and to the processus lateralis of the same cornu. Below the level of the internal accessory olivary bodies the same grey masses give off anterior roots of the first pair of cervical nerves, which above these olivary bodies give off hypoglossus roots. The vagus of Man is, on the other hand, connected with grey masses homologous with the posterior grey cornu in part. The hypoglossus and spinal accessory of the Mammalia being thus so clearly connected anatomically with grey masses representing the anterior grey cornu in the spinal column, it is only reasonable to suppose that *both alike* are homologous anatomically with anterior nerve-roots. The spinal accessory will therefore have to be sought most probably in the anterior roots of the vagus.

In the second place, there is the fact to be taken into consideration, that the 'elevator' of the shoulder-girdle is supplied by an anterior vagal root in Echinorhinus and in Spinax by branches from the vagus *after it has been joined by the two anterior roots.* It is possible that this muscle corresponds more or less closely with the mass from which our trapezius and sternocleido-mastoid are differentiated. This fact would therefore also make for the derivation of the spinal accessory from the anterior vagal roots, as well as the hypoglossus, which is without doubt so derived.

The close union in Echinorhinus of the anterior roots of the vagus with the first spinal nerves certainly lends strength to the homology between these roots and the spinal accessory and hypoglossus. On the one hand in Mammalia the vagus is intimately connected with the spinal accessory. Indeed, evulsion of this latter nerve is said to paralyse all the motor fibres contained in the vagus (Hermann, *Grundriss*, p. 331). It is also connected with the hypoglossus. It is this connection that we see exaggerated in Hexanchus, Spinax and Carcharias. On the other hand, the vagus in Man is connected with the suboccipital nerve (*Q. S.* p. 636), the spinal accessory is connected with the cervical plexus, and the hypoglossus receives the well-known communicans noni. It is this connection that we find exaggerated in Echinorhinus. We may suppose it carried still further—even to the suppression of the anterior roots as *visible external* roots. Then we should be able to explain how it is in Amphibia that the *first spinal* nerve represents the hypoglossus, being distributed to the hyoidean and tongue-muscles. The distribution in Teleostei of branches derived from the first spinal nerve to the homologous region led Cuvier and Büchner long ago to designate that nerve as hypoglossus, while Stannius pointed out more correctly that it represented this nerve *in part*. It is of course possible that the deep origin of the first spinal nerve may in these cases embrace that of the anterior vagal roots, *i. e.* extend far forwards into the medulla oblongata. This point, however, is one which does not appear to have attracted observation; but that the supposition is far from improbable may be surmised from the great variations both in the number of the roots, and of the place of exit, displayed by the first spinal nerves (*St.* p. 121). It is also possible where two distinct sets of nerves come to supply identical regions from great morphological changes, that in given cases one set may disappear, the other persist and develope, and *vice versâ*.

The accompanying table displays at one view the relations of the cranial nerves to the visceral arches and clefts, as well as the special homologies suggested in this paper.

The spinal column is not much differentiated[1]. The core is composed of dense fibrous tissue: a complete fibrous septum is developed at intervals, at a spot corresponding to the exit of the anterior roots of the spinal nerves. In this way a series of oblong chambers is constituted internally, and these enclose the gelatinous remains of the notochord. On the ventral surface of this fibrous core, semi-rings of cartilage are developed, thickened

[1] In this description the present tense is used where the part described has been preserved.

Arch. No.	Name.	*Cleft.*	*Nerve.*	*R. dorsalis.*	*R. ventralis.* a = anterior, p = posterior } division.	*R. pharyngeus.*
I.	Trabeculæ cranii.		Prætrabecular = Ophthalmic.	Nervus recurrens of Arnold.	Frontal branches, and orbito-nasal.	*Absent in these nerves.*
II.	Palato-pterygoid.	Lacrymal.	Præpalatine = Sup. Maxillary.	Several Rr. dorsales from common trunk of conjoined nerves = nervi recurrentes of Arnold and auriculo-temporal (?) = intracranial nerves of Teleostei.	a = naso-palatine. p = spheno-palatine and infra-orbital.	
III.	Meckel's Cartilage.	Mouth.	Præmeckelian = Inf. Maxillary.		a = buccal (?). p = Gustatory + Dental.	
IV.	Anterior Cornu of Hyoid.	Spiracle Eustachian Tube.	Præhyoidean = Facial.	Auditory (Gegenbaur).	a = præspiracular nerve (= pharyngeal branch of Vidian ?). p = Chorda Tympani + main stem in Man.	= Palatine nerves in Fishes. = Petrosal nerves in Man.
V.	Posterior Cornu of Hyoid = 1st Branchial Arch.	1st Branchial Slit.	1st Præbranchial = Glossopharyngeus.	Communicating branch to the auricular nerve.	a = main stem in Man. p = œsophageal branches.	Pharyngeal nerve = R. communicans in Sturgeon = Jacobson's nerve in Man.
VI.	2nd Branchial Arch.	2nd Branchial Slit.	2nd Præbranchial = 1st Branchial nerve of Vagus.	Auricular nerve.	a = R. anterior. p = R. posterior.	R. pharyngeus.

laterally, and forming short conical processes to which are attached the stunted cartilaginous ribs. The floor of the neural canal is fibrous, its sides are formed by cartilage. There is a series of crural cartilages, triangular in shape, and pierced by the anterior roots of the spinal nerves. Between these fit in large 'intercrurals,' also triangular in shape, the apices touching the fibrous core, as in Notidanus, Centrina, &c., and pierced by the posterior roots of the spinal nerves. At the summit of each crural cartilage and between each intercrural is a small cartilage, lozenge-shaped in transverse section.

There is little to say about the digestive organs after the description given by Professor Turner (IX. pp. 299—300 of this *Journal*). There is no duodenal dilatation, and duodenal cæca are absent. The spiral fold of the intestine, which is at first straight, but gradually becomes oblique, commences by a forked extremity, the fork embracing the pyloric aperture. The mucous membrane of the rectum is smooth. The length of the duodenum and valvular intestine in the female specimen was 23½ inches. The liver consisted of two equal lobes; in the female 4 ft. 3 in. long, weighing together 21 lbs. 12 oz., and of so low a specific gravity that they floated readily on water. There was a large gall-bladder containing some liquid yellow bile. The pancreas is a large bilobed gland; one lobe simple and thin, the other and larger lobe thick and bifid at the extremity. The longer of the two bifurcations curves round the pyloric extremity of the stomach just at the commencement of the duodenum. The bile and pancreatic ducts open into the duodenum below the commencement of the spiral valve.

In the digestive tract were found several examples of a large Distomum—species undetermined as yet.

The conus arteriosus gives rise to a long aortic stem, from which spring the branchial arteries, four in number, the anterior bifurcating, as is usual in Selachians. It contains four rows of valves. Of these the anterior or first row contains the largest valves, three in number. The second row has very small valves indeed, easily overlooked, one behind each of the valves in the first row. A fourth minute valve is intercalated in this row. The third and fourth rows each contain four valves, those in the third rather the larger. In shape they are broad, not deep, and they vary in size, two valves being larger than the other two. The ventricle has thick walls, with strongly marked internal muscular ridges. The auricle and sinus venosus have each their usual bivalved aperture.

There is a heart-shaped spleen attached to the curvature of the stomach. A second spleen, pyriform in shape, and in the female specimen about eight inches long, lies close to the pancreas.

Just below (in the natural position of the animal) the terminal division of the branchial artery, lying between the sterno-hyoid muscles (of Owen), there was an elongated slender structure, reddish in colour, and somewhat resembling atrophied thymus as it appeared on microscopical examination. It probably represents the thyroid.

A similar gland, reaching right across the body, lay close behind the branchial arches, thrusting itself between the œsophagus and the vertebral column. Its microscopic appearance was similar to that of the gland just mentioned. It is usually held to represent the thymus.

In the female the kidneys reached to within a foot of the apex of the heart. The two ureters dilate terminally and open separately into the cavity of the urethral papilla which projects from the dorsal wall of the cloaca. In the male the whole of the outer side of the vas deferens shows traces of kidney-substance, but it is only posteriorly that the characteristic colour of the kidney is evident, the forepart being colourless.

The ovaries are large, and consist of a loose stroma, embedding ova of every size, some quite microscopic, others of the size of ordinary pistol-bullets, and one fully as large as a hen's egg. They lie close behind the oviducts.

The oviducts were suspended each by a separate peritoneal fold, which coalesced with its fellow to form a single lamina before it was attached to the vertebral column. The mesogastrium commenced at the point of junction of the two oviducal folds. The upper part of the oviduct has a thin mucous membrane, elevated into numerous, close-set, and fine folds, somewhat sinuous. At the summit of each fold is a row of minute orifices (glandular no doubt) quite visible to the naked eye. A large nidamental gland was present, about 2 in. in transverse diameter, and 1½ in. broad. Professor Turner appears not to have found this gland in his specimen (IX. p. 299 of this *Journal*), though, according to Bruch (*Études sur l'appareil de la* *génération chez les Sélaciens,* Strasbourg, 1860), it is always present: *La glande de l'oviducte est constante,* p. 64. It is (p. 54) even present in viviparous species. The upper third of this gland is greyish in colour and apparently smooth, while the lower two-thirds is yellowish, and consists apparently of a number of transverse, thin, close-set, and parallel folds, between which, Bruch (p. 52) asserts, are situated the orifices of glands. The nidamental gland appears to vary much in size in different Selachians, and in the same species at different times of the year, being much larger at the period of sexual activity. It appears also that the relative arrangement of the grey and yellow zones is not always the same (cf. Bruch, pp. 51, 52). In our specimen the nidamental gland was situated 28 inches from the outlet of the oviduct.

The oviduct (uterus) below the nidamental gland has a thick mucous membrane produced into short wavy villous folds. These folds are aggregated more or less distinctly into four rows. In each row the central folds are well developed, while on each side they are stunted and feeble.

The mucous membrane at the termination of the oviducts is much more smooth, and has only a few papillæ. The apertures lie one on each side the cloaca. They are large, large enough indeed to admit two fingers easily: a point in which our specimen again differs from Professor Turner's, which from the minuteness of the ova, and the capillary size of the orifices of the oviducts, was not in a state of sexual activity. In the middle line between the oviducal apertures there lies below, the round rectal aperture; above, the long conical urethral papilla.

The abdominal pores in both specimens are large and slitlike, situated just without the rim of the cloaca at the base of the ventral fins and guarded by a fold of skin.

In the male the testes are thin, dark-coloured glands about 8 inches in length and much flattened. They are suspended by a well-developed peritoneal fold. The vas deferens is slender at its commencement from the epididymis, and much convoluted in the usual way. Lower down it becomes straight and of greater calibre, and terminally each has a well-marked and separate dilatation with thick muscular walls, and feebly marked internal rugæ. The vas deferens on each side opens separately into the cavity of the genito-urinary papilla, situated on the dorsal wall of the cloaca (cf. Bruch, *op. cit.* pp. 35, 36, and Pl. I. Figs. 1 and 2).

The claspers are large, about 5 inches in length. On their inner and posterior side is a slit about 2½ inches long, which leads into a deep conical cavity (cf. Owen, *Comp. Anat. Vert.* Vol. I. pp. 570, 1).

DESCRIPTION OF PLATE VII.

Fig. 1. The Brain of Echinorhinus Spinosus.

Olf. Rhinencephalon—Olfactory Tracts. *C.* Procencephalon. *Th.* Thalamencephalon. *Op.* Optic Nerve. *C. B.* Mesencephalon—Corpora Bigemina or Optic Lobes. *Ce.* Cerebellum. *M. O.* Medulla Oblongata. *L. Tr.* Lobi Nervi Trigemini. *Pi.* Pineal Gland. *V* 3. Third Ventricle. *V* 4. Fourth Ventricle: the roof thick in front, thin behind. *s.* Outermost strand of Medulla Oblongata. *g.* Ganglionated Tract. *p'.* Teretial (?) Tracts. *p.* Anterior pyramids. III. Oculomotor. IV. Trochlear. V. Trigeminus. V*a*. First root of Trigeminus. Vβ + Vγ. Second and Third roots. VII. Facial. *Au.* Auditory Nerve. IX. Glossopharyngeus. X. Vagus (posterior roots). X'. Vagus (anterior roots—two last only represented). *Sp.* I. First Spinal Nerve.

Fig. 2. Fifth and Seventh Nerves (semi-diagrammatic).

Vα. First root of Fifth; Vβ. Second root. Vγ. VII. Third root and root of Seventh. V. Trigeminus. *Opth.* Ophthalmic. *d. d.* R. dorsalis. *Opth'.* Ophth. superficialis (frontal). *o. n.* Ophth. profundus (orbito-nasal). *Ci.* Ciliary Nerve. *tr.* Terminal twigs to upper (dorsal) surface of rostrum. *d'.* R. dorsalis. *mx.* Superior Maxillary Nerve. *n. p.* Anterior division (=naso-palatine). *s. pa.* Spheno-palatine, and *I. o.* Infra-orbital, = posterior division. *Mn.* Inferior Maxillary Nerve. *b.* Buccal (?) Nerve. *au.* and *P. M.* Muscular Nerves. *Mn'.* Gustatory + Inferior dental. VII. Facial. *d''.* R. dorsalis. *Sp.* Spiracular Nerve. *pt.* Palatine Nerve. *h. br.* Muscular Nerves. *an.* Nerve to angle of mouth. *ch.* R. mandibularis internus (chorda tympani). *F.* R. mand. externus (=main trunk).

Fig. 3. Glossopharyngeal, Vagus and First Spinal Nerves (semi-diagrammatic).

Gp. Glossopharyngeal; *d.* R. dorsalis; *d**. Muscular (?) Nerve; *br.* Hyoidean (anterior) branch. *Ph.* Pharyngeal Nerve; *br'.* Posterior division (branchial). *Vg.* Posterior (dorsal) roots of Vagus; *d'. d''.* Rr. dorsales. *L.* Lateral line Nerve. *Br.* I. II. III. IV. Branchial Nerves; *a.* and *p.* Anterior and posterior divisions; *m. m'.* Muscular branches; *ph'.* Pharyngeal branches. *ph''.* Pharyngeal branch of IVth Branchial Nerve (= main portion). *v.* Twigs to mucous membrane of Vth arch. *an.* Anastomosis with I. *m''.* Muscular Nerve of Posterior division of IVth Branchial Nerve. *m'''.* Muscular Nerve from main trunk of Vagus. *oe.* Œsophageal branches. *I. I.* Visceral branches. *Vg.* I. II. III. IV. Anterior Vagal roots. *d'''.* Branches to Muscle. *v'.* Ventral branches. *Sp.* I. First Spinal Nerve; *A.* and *P.* Its anterior and posterior roots; *ds.* R. dorsalis. *as.* Branch to ganglion from anterior root. *ps.* Branch from ganglion to anterior root; *v''.* R. ventralis. *Sp.* II. III. IV. V. Spinal Nerves—Rr. ventrales. *an'.* Anastomosis of Cervical Cord with Muscular Nerve of Vagus. *Cv.* External, *Cv'.* Internal, division of Cervical Cord.